

**PALORCHESTES SELESTIAE, A NEW SPECIES OF PALORCHESTID MARSUPIAL
FROM THE EARLY PLIOCENE BLUFF DOWNS LOCAL FAUNA, NORTHEASTERN
QUEENSLAND**

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Palorchestes selestiae sp. nov. from the early Pliocene Bluff Downs Local Fauna is described on the basis of an isolated LM¹. It is larger than *P. painei* and *P. parvus* but smaller than *P. azael* in both length and width of lophs. It is also differentiable from all other palorchestids on the basis of the combination of links between, or stemming from lophs. It is the second undoubted Pliocene species and shares features of both *P. parvus* and the Pleistocene *P. azael*. With its relatively derived anterior morphology and plesiomorphic posterior morphology, *P. selestiae* challenges current notions about the phylogenetic relationships of diprotodontid marsupials which suggest that small size and simple structure are probably plesiomorphic features. □ *Palorchestes, palorchestids, Bluff Downs Local Fauna, Pliocene, Diprotodontia, Marsupialia*.

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Palorchestes was described by Owen (1873) on the basis of an anterior portion of a cranium including the rostrum. The holotype was obtained by Dr Ludwig Becker and described by Owen (1874) as *P. azael* from an unspecified deposit in Victoria interpreted by Mahoney & Ride (1975) as the River Tambo in Gippsland. Owen (1873:387) considered *Palorchestes* to be "... the largest form of kangaroo hitherto found".

Owen regarded *Palorchestes* to be a macropodid, a view followed by Simpson (1945) who placed the genus within the subfamily Macropodinae. Raven & Gregory (1946), however, placed it in the subfamily Sthenurinae while Tate (1948) placed it in a new subfamily of kangaroos, the Palorchestinae. Woods (1958) was the first to recognise the diprotodontid rather than macropodid affinities of *Palorchestes*. Archer & Bartholomai (1978) followed this assignment but elevated Tate's Palorchestinae to family level.

Palorchestes selestiae sp. nov. is described here on the basis of an isolated LM¹ from the fluvial and lacustrine deposits of the Allingham Formation, northwest of Charters Towers, northeastern Queensland. This formation contains a diverse assemblage known as the Bluff Downs Local Fauna, and has been the subject of many studies, most recently including those of Vickers-Rich (1991), Mackness et al. (1993), Boles & Mackness (1994) and Mackness (in press). Archer & Wade (1976) assigned an early Pliocene age to the assemblage on the basis of the interpreted age of the overlying Allensleigh Ba-

salt. Archer, in Archer & Wade (1976) noted, but did not name three other diprotodontoids from the Bluff Downs Local Fauna, a species of *Euryzygoma*, a species of *Zygomaturus* and an unidentified 'notothere'.

TERMINOLOGY

Dental homology of cheekteeth follows Lockett (1993) such that the first adult molari-form tooth is M¹ and the deciduous molariform tooth is dP³. Terminology of crown morphology (Fig. 1) follows that used by Archer (1976) except that the metaconule is used instead of hypocone following Tedford & Woodburne (1987). The-gotic terminology used follows Every (1972). Abbreviations for specimen numbers: QMF, Queensland Museum fossil collection; UCMP, University of California, Berkeley; P, South Australian Museum.

SYSTEMATICS

- Order DIPROTODONTIA Owen, 1866
- Suborder VOMBATIFORMES
Woodburne, 1984
- Infraorder VOMBATOMORPHIA
Aplin & Archer, 1987
- Family PALORCHESTIDAE (Tate, 1948)
Archer & Bartholomai (1978)
Palorchestes Owen, 1873

TYPE SPECIES

Palorchestes azael Owen 1873.

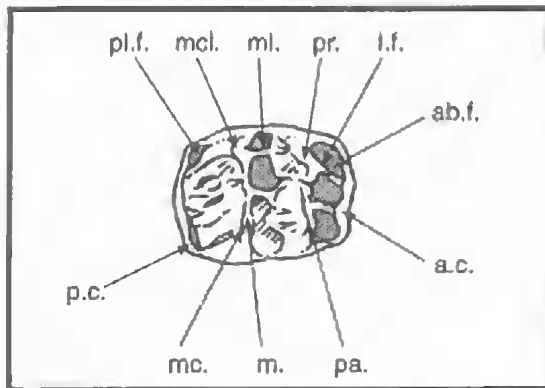


FIG. 1. Diagram showing terminology of an M^1 of *P. selestiae*. Regions used for measurements in Table 1 are also presented using the holotype (QMF12455). Arrow indicates anterior of molar. Abbreviations: ab.f. anterobuccal fossa; a.c. anterior cingulum; l.f. lingual forelink; m. metaloph; mc. metacone; mcl. metaconule; ml. midlink; pa. paracone; p.c. posterior cingulum; pl.f. posterolingual fossa; pr. protocone.

Palorchestes selestiae n. sp.
(Fig. 2)

MATERIAL EXAMINED

HOLOTYPE: QMF12455, an isolated LM^1 , Main Quarry (19° 43'S, 145° 36'E), Allingham Formation, Bluff Downs Station, northeastern Queensland.

ETYMOLOGY

For Selesti Smith of Bluff Downs Station.

DIAGNOSIS

Small LM^1 with lingual forelink terminated in the cingular valley and not in contact with the cingulum; second incipient buttress on the back of the metaloph; posterolingual fossa well developed; posterior cingulum rises to an apex mid-length; incipient buttressing on the posterior wall of metaloph; one midlink and two incipient midlinks; double forelinks.

DESCRIPTION

The holotype consists of a complete, relatively unworn LM^1 , lacking any remnant of the roots. The metaconule is the tallest cusp with the protocone, paracone and metacone subequal in height. Protocone linked to the paracone by a well-defined sinuous protoloph. Metaconule linked to the metacone by a well-defined crescentic metaloph whose ends are posteriorly deflected.

The anterior cingulum fails to extend around the base of the protocone. A slight anterobuccal cingulum is continuous with the anterior cingulum. Otherwise there are no lingual or buccal cingula. Anterior cingulum high resulting in deep fossae where the forelinks join the cingulum. Posterior cingulum closer to the metaloph than the anterior cingulum is to the protoloph. As a result, the posterior cingular valleys are not as deep as the anterior ones. There is a conspicuous interproximal wear facet on the anterobuccal corner of the tooth, presumably caused by abrasion against P^3 .

There are a number of blades on the crown. Where the enamel has been breached, both sets of leading and trailing blades (*sensu* Every, 1972) can be seen on the protoloph and metaloph. A number of secondary blades are also present. One blade (the apical margin of the lingual forelink) leads from the protocone to the anterior cingulum. Another blade (the apical margin of the buccal forelink) connects the protoloph, approximately one third of the way between the paracone and the protocone, to the anterior cingulum. A well-developed primary midlink joins the protoloph to the metaloph. The posterior end of this midlink contacts the trailing edge of the

TABLE 1. Comparative measurements of *Palorchestes* M^1 in mm.

Specimen	No.	L	AW	PW
<i>P. selestiae</i>	Holotype	22.6	16.6	16.9
<i>P. parvus</i>	QMF784(cast)	20.7	15.7	15.4
	QMF12476		15.4	15.3
	QMF2963	19.3	14.9	14.4
	QMF3719(cast)	19.3	15.0	14.2
	QMF2967	19.4	15.6	15.6
	QMF2965	20.9		14.5
	QMF789	19.5		
<i>P. cf parvus</i>	P24097 (R)	18.8	13.6	12.9
	P24097 (L)	18.6	13.9	13.6
<i>P. azael</i>	QMF772 (cast)	26.6	21.9	21.5
	QMF3837	25.8	20.7	19.7
	P31370	28.3	21.8	21.4
	P31371	28.3	22.6	21.9
	P31372	26.1	22.9	21.9
<i>P. painei</i>	UCMP70553(R)	16.5*	13.6*	13.8
	UCMP70553(L)	16.8	14.4	13.7
	UCMP70550(R)	16.7	13.9*	13.7
	UCMP66521(L)	17.8	14.0*	13.2*

* = approximation

TABLE 2: Summary of links in *Palorchestes* M¹
 () Incipient link; - Link/s worn, * cast.

Specimen	No.	Forelinks	Midlink	Hindlinks
<i>P. selestiae</i> sp. nov.	Holotype	2	1(1)	(2)
<i>P. parvus</i>	QMF784*	2(1)	2	2
	QMF12476	2	2	
	QMF2963	2(1)	2	2
	QMF3719*	2	2	2
	QMF2967	2	2	2
	QMF2965	2	2	
<i>P. azael</i>	QMF772*	2	1(2)	0
	QMF3837	2	1	0
<i>P. painei</i>	UCMP70553	1	1	1
	UCMP66521	1	1	1

posterior metaloph blade. Another less developed midlink occurs on the lingual side of the tooth. This smaller link is steeply v-shaped rather than shallowly v-shaped as is the primary midlink. There is a very deep fossa between these two midlinks.

There is also a swollen buttress on the posterior flank of the proto-loph, buccal to the primary midlink. Another steeply inclined buttress descends posteriorly to the posterior cingulum from the tip of the metaconule and supports an incipient blade that connects the apex of the metaconule to the posterior cingulum. A smaller blade-like structure is present on the posterior wall of the metaloph, buccal to the primary posterior blade. There is some slight crenulation of the enamel at the base of the lophs.

REMARKS

P. selestiae is approximately 3/4 the size of *P. azael* Owen and is 1/5 larger than *P. parvus* De Vis. Whilst closer in size to *P. parvus*, *P. selestiae* is morphologically closer to *P. azael*. *P. azael* differs in that the lingual forelink links the protocone to the anterior cingulum, and lacks the second incipient buttress on the back of the metaloph. *P. selestiae* has a better developed posterolingual fossa and the apex midlength on the cingulum is absent in *P. azael*. In *P. parvus* the anterobuccal fossa is less developed, both forelinks join the anterior cingulum, there are two well-defined hindlinks which join directly with the posterior cingulum, and two midlinks are present. *P. panei* Woodburne has a definite midlink, absent in *P. selestiae*, and it lacks the double forelink and the two incipient buttresses on the posterior wall of the metaloph.

PHYLOGENETIC AFFINITIES

The early Miocene *Nagapakaldia tedfordi* and *Pitikantia dailyi* (Stirton, 1967) from the Tirari Desert of South Australia have previously been regarded as the pleisomorphic sister group (subfamiliae Incertae) of the apparently more derived Palorchestinae based on synapomorphies in the auditory region and neurocranium (Stirton et al., 1967). It has been further suggested by Stirton et al. (1967:154) that *Pitikantia* "... is much nearer, if not in, an ancestral position to *Palorchestes*". Archer (1984), however, observed that there was little evidence to regard the two groups as monophyletic, with species of *Ngapakaldia* and *Pitikantia* lacking the specialized molars and retracted nasal bones of palorchestines, even though their basicranial morphology was similar. Murray (1986) described the middle Miocene *Propalorchestes novaculacephalus* from the Bullock Creek Local Fauna and, based on its cranial base, glenoid fossa morphology and auditory region, placed it within the subfamily Palorchestinae. Subsequently, Murray (1990) described the dentition of *P. novaculacephalus* as well as a new taxon, *P. ponticulus* from D-site (System A), Riversleigh, Queensland. The latter was also placed within the Palorchestinae.

The M¹, the most diagnostic tooth for palorchestids (Woods, 1958; Woodburne, 1967), is characterised by elaborated fore-, hind- and midlinks. These features are lacking in species of *Ngapakaldia* and *Pitikantia* but present or incipient in *Propalorchestes novaculacephalus*, considered to be the sister group of *Palorchestes* Murray (1986, 1990). *Palorchestes painei* has the simplest system of links with one fore-, one hind, and one midlink which is the condition also seen in *P. novaculacephalus*. All other species of *Palorchestes* have two forelinks as a synapomorphy.



FIG. 2. *Palorchestes selestiae* holotype QMF12455. Actual size. Occlusal view stereo pair. Anterior at top.

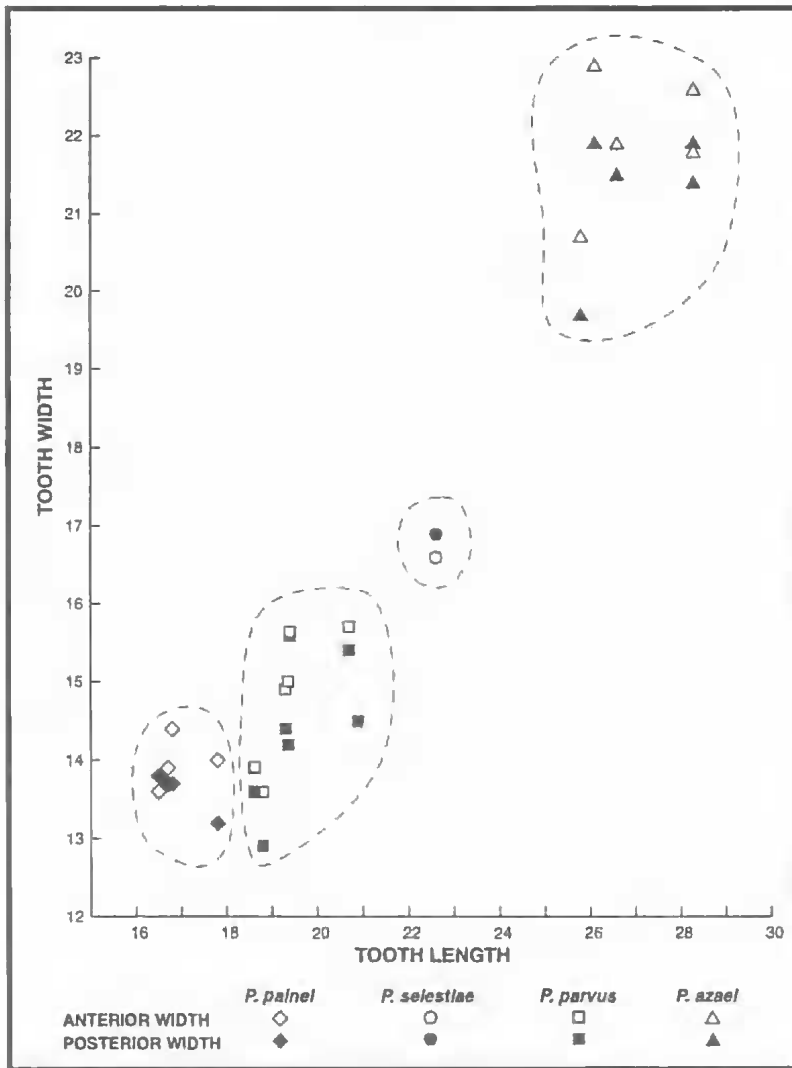


FIG. 3. Bivariate plots of tooth length against anterior width (") and tooth length against posterior width M^1 of *Palorchestes* species.

Palorchestes selestiae and *P. azael* share accessory midlinks and the reduction of hindlinks as synapomorphies while *P. parvus* has two hindlinks and two midlinks as autapomorphies. The development of accessory hindlinks and the lingual forelink not extending to the anterior cingulum in *P. selestiae* are considered autapomorphies for this taxon.

Palorchestes selestiae indicates need for caution in determining phylogenetic relationships within diprotodontoid lineages based on size alone. Stirton *et al.* (1967) suggested that molar size and complexity in diprotodontoids were in-

verse correlates of age. By those measures, *P. painei*, as the smallest species, ought to be the oldest followed, in decreasing age and increasing size by *P. parvus*, *P. selestiae* and *P. azael*. However, *P. selestiae* comes from a demonstrably early Pliocene site, whereas the smaller *P. parvus* comes from early to middle Pliocene sites which does not support the biostratigraphic argument of Stirton *et al.* (1967).

Several authors (Archer, 1976b; Murray, 1990) have proposed that the bilophodont upper molars of species of *Palorchestes* are derivable from subselenodont animals such as wynyardiids. Murray (1990:49) suggests "...The possibility of paraphyletic bilophodony could not be ruled out, particularly with respect to the diprotodontids". In this view those animals such as the late Miocene *P. painei* which had the least development of selenodont features would be regarded as the most derived. It would then follow that, barring convergence, the more elaborate the cresting, the more plesiomorphic the animal. The selenodont groundplan is still evident in *P. selestiae*, even though it has been obscured to some degree by the development of lophs.

PALAEOECOLOGY

Palorchestids are uncommon elements in most Australian marsupial faunas although they have a long Tertiary and Quaternary history (Murray, 1991). The oldest known representatives are species of *Ngapakaldia* and *Pitikantidia* from the Oligo-Miocene deposits of central Australia and Riversleigh in northwestern Queensland. At the younger end of their time range, some may be

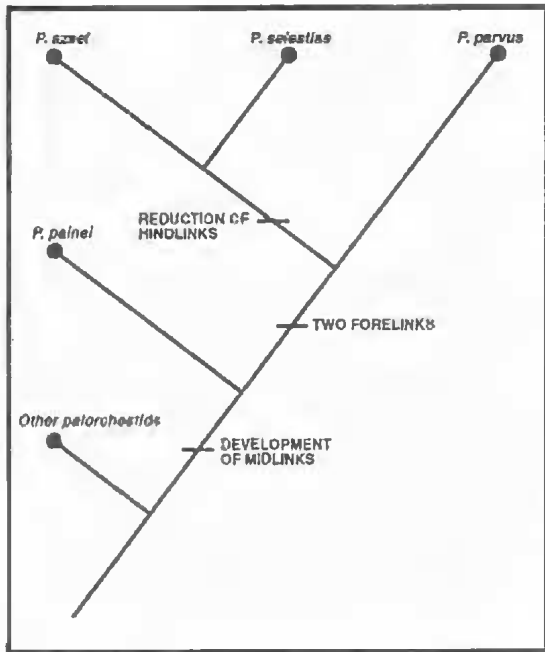


FIG. 4. Cladogram of taxa based on M¹ morphology.

only 30 000 yBP (Murray, 1991) and it has been suggested that *Palorchestes* was contemporaneous with humans. Murray & Chaloupka (1984) have interpreted an Aboriginal rock painting in the Arnhem Land escarpment as a possible rendition of a species of *Palorchestes* although this has been questioned (Lewis, 1986; Chaloupka & Murray, 1986; Mackness, 1992).

The reduction and retraction of the nasals, along with a conspicuous fossae for large *nasomaxillolabialis* muscles and a narrow, protracted rostrum have been used as a basis for reconstructing palorchestids with a trunk and the basis of their popular description as 'marsupial tapirs' (Bartholomai, 1978; Flannery, 1983; Flannery & Archer, 1985; Murray, 1991). The long, narrow deeply grooved symphysis suggests that palorchestids had long protrusible giraffe-like tongues (Murray, 1991). The spatulate lower incisors are almost parallel to strongly developed diastemal crests and interpreted by Murray (1991) as probably being used to strip leaves or crop clumped vegetation. Little has been published about the postcranials of palorchestids. Woods (1958) cast doubt on the association of postcranials with skull remains suggested by several authors (Owen, 1876; Gregory, 1902; Fletcher, 1945). Archer (1984), however, has noted that *Palorchestes* has powerful forelimbs

equipped with large laterally compressed claws. Flannery & Archer (1985) have used postcranial material and teeth to attempt a reconstruction of two species. Their analyses suggested the possibility that species of *Palorchestes* were medium-sized folivores that may have used their powerful claws and arms to rip bark off trees for food or to uproot shrubs with tuberous roots.

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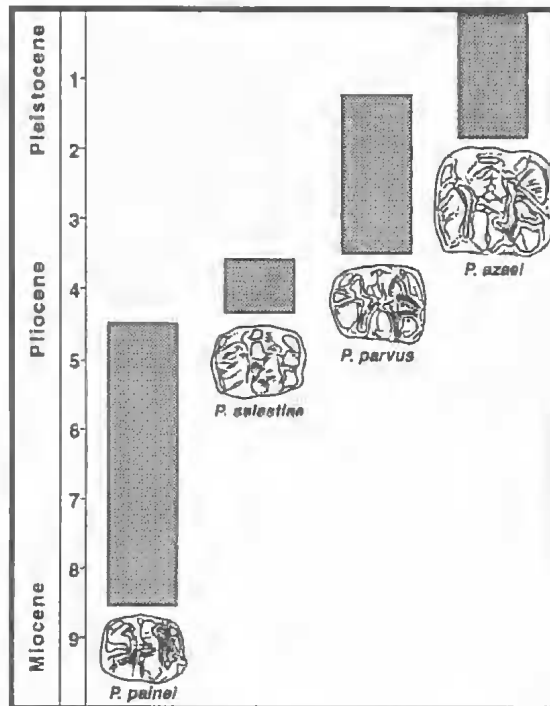


FIG. 5. Distribution of species of *Palorchestes*.

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